

## Chapter Thirteen

# *Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States*

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### **13.1 DEFINITIONS, REGIONAL MARSH CHARACTERIZATION AND LARGE-SCALE PATTERNS**

#### **13.1.1 Introduction**

We use the term nekton (organisms capable of active swimming) to include both fishes and macrocrustaceans (crabs, shrimp). Direct use of saltmarsh habitats by nekton is linked to geomorphology via the physical processes that determine estuarine landscapes or environments. The physical processes include sediment deposition and redistribution, delta-building, sea level change, and the action of currents and tides. Landforms in turn are influenced by climate. Climate affects salinity regimes at the scale of the estuary and the region: climate affects vegetation type and stature directly through the balance between rainfall and evaporation. Tidal range combined with slope of the intertidal zone determines both the area inundated and the depth of inundation. Tidal regime coupled with large-scale

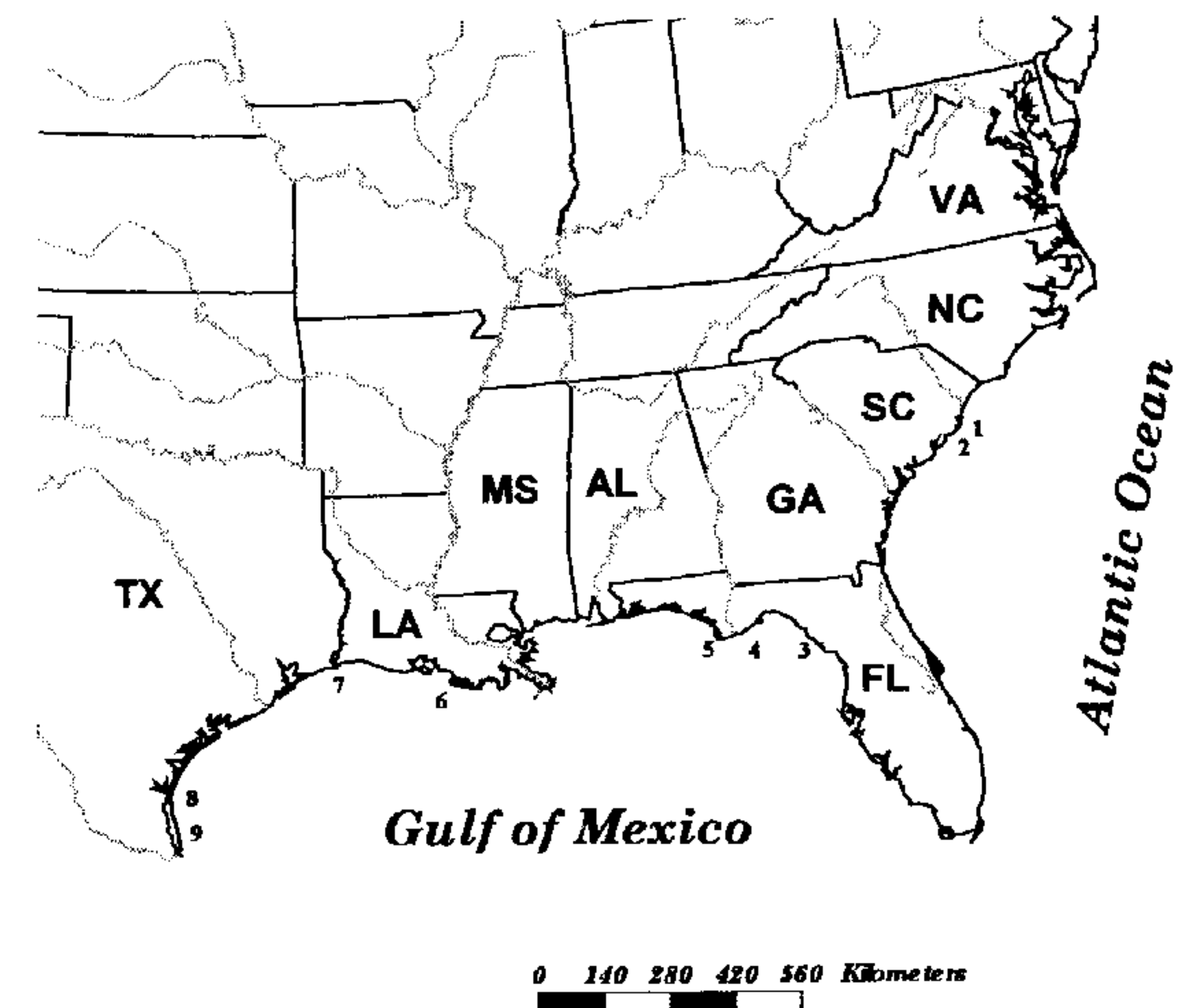
meteorological forcing functions determines the pattern and duration of marsh flooding. Relative sea level change combined with sediment supply determines whether shorelines are subsiding, accreting, or remaining relatively constant in terms of area.

In this review of patterns of nekton use of intertidal saltmarshes, our purpose is threefold: (1) to summarize the knowledge on taxa using the marsh surface; (2) to analyze patterns of distribution and abundance as they relate to geomorphological features of the marsh; and (3) to examine the ways in which nekton link intertidal and subtidal habitats. Geomorphological features of saltmarshes considered herein include position along a gradient of stream order (*sensu* Horton 1945), subtidal geomorphology, marsh elevation and flooding duration, drainage density, and relative amount of edge.

The review has an acknowledged North American bias because most of the literature on saltmarsh nekton is from this geographic area. Further, the majority of such studies have been conducted within the region of most extensive saltmarsh development, from the mid-Atlantic coast to the northwest coast of the Gulf of Mexico. This review therefore focuses on this region, though we refer to studies in other locations when appropriate. We have chosen to focus on the vegetated intertidal portion of saltmarshes, i.e. the marsh surface, both because of recognition that this portion of the marsh has direct habitat 'value' for nektonic organisms, and because recent sampling innovations have permitted the quantitative testing of a number of hypotheses about the relationship between nekton distribution and geomorphological and hydrological features of saltmarshes. Although the review focuses on saltmarshes, we include research from the tidal freshwater portion of the estuary where that research elucidates the geomorphological theme. Finally, we have largely restricted our discussion to natural, relatively unimpacted marshes. Consideration of impounded, constructed, and degraded marshes is beyond the scope of this review.

### 13.1.2 Characterization of saltmarsh development in different ecoregions

Most southeastern Atlantic estuaries (Virginia–North Carolina border to the Georgia–Florida border) are classified as coastal plain saltmarsh estuaries (Figure 13.1). Most lack a major river source, except North and South Santee rivers, South Carolina, and Charleston Harbor, South Carolina (Dardeau et al. 1992). There are extensive, well defined drainage networks, dendritically intersecting extensive coastal saltmarshes. Typically, open water area is less than 20% of the estuary (Kjerfve 1989). Saltmarshes are extensive and dominated by *Spartina alterniflora* in regularly flooded marshes. *Juncus roemerianus* marshes occur at higher elevations, where salinity of interstitial water is lowered, or where flooding frequency is irregular (Dardeau et al. 1992). Within this region, saltmarshes are most extensive in Georgia (167 400 ha) and South Carolina (165 167 ha) (Dardeau et al. 1992). Tidal regime is semidiurnal; tidal range is 2–3 m in the middle of the



**Figure 13.1** Southeastern US coastal zone. Numbers refer to geographic locations mentioned in the text: 1, North and South Santee Rivers; 2, Charleston Harbor; 3, Suwannee River; 4, Apalachicola Bay; 5, St Andrews Bay; 6, Atchafalaya Bay; 7, Sabine Lake; 8, Baffin Bay; 9, Laguna Madre

Georgia coast at Sapelo Island, and decreases to <1 m both north and south (Wiegert and Freeman 1990; Dardeau et al. 1992). Greater tidal amplitude in Georgia results in more extensive development of natural levees along creek banks (Dardeau et al. 1992), a geomorphological factor that has received little attention as it relates to marsh use by nekton.

Saltmarshes of the northern Gulf of Mexico coastline (Suwannee River, Florida to the Texas–Louisiana border) are extensive, covering about 2.1 million ha (Figure 13.1) (Dardeau et al. 1992). Regularly flooded marshes are dominated by *Spartina alterniflora*. Such marshes are best developed in the Mississippi deltaic plain in Louisiana. Much of the Mississippi, Alabama, and Florida coast (within the northern Gulf) are dominated by *Juncus roemerianus* marshes. Such marshes are characterized by less frequent flooding from predominantly wind-driven tides (as opposed to predictable lunar tides). In these *Juncus* marshes, *S. alterniflora* occurs only in a narrow band adjacent to tidal creeks or other open water (Dardeau et al. 1992). Mixed tides (two unequal high and/or two unequal low waters each tidal day) occur from Suwannee River to Apalachicola Bay, Florida and from Atchafalaya Bay to Sabine Lake. Diurnal tides (one high and one low/day) occur from St Andrews Bay, Florida west through the Mississippi Delta region (Dardeau et al. 1992). Throughout the northern Gulf region, the tidal range is small,

averaging approximately 0.30 m at the coast within the Mississippi deltaic plain, for example. Seasonal changes in water level are pronounced with the result that in coastal Louisiana, *S. alterniflora* marshes are flooded only about 20% of the time in January, but up to 80% of the time in September and October (Gosselink 1984). Regularly flooded saltmarsh is also locally extensive along the upper Texas coast, but decreases in areal extent in south Texas where *S. alterniflora* occurs mostly as narrow fringe marsh along major water courses. *S. alterniflora* is essentially absent along the margins of Laguna Madre and Baffin Bay (Webb 1982).

### 13.1.3 Major families using marsh-surface habitats

We compiled a list of numerically dominant fish and decapod crustacean species collected in marsh-surface habitats as reported from studies of Gulf of Mexico and Atlantic coastal marshes (Table 13.1). We stress that studies that collected fauna from marsh creeks are not included. We classified a species as numerically dominant in a study when it was reported as one of the five most abundant of a taxonomic group (fishes or crustaceans) and represented >1% of the total catch in that group.

Limitations to these data are several. Published studies of marsh habitat use by nekton are restricted in geographic extent. Most research has been conducted in estuaries of the northern Gulf of Mexico. A few studies of Atlantic coastal marshes, including those in tidal freshwater reaches of the estuary, have been completed. However, other than Chamberlain and Barnhart (1994), we are unaware of any published studies of nekton use of the vegetated surface of natural marshes of the Pacific coast. In none of the geographic regions have the nekton associated with the marsh surface been described in all of the different marsh types that exist. For example, on the Gulf coast, direct use of tidal freshwater marshes by nekton has not been studied, and few studies have been conducted in oligohaline and polyhaline environments (Table 13.1). Studies of the marsh surface on the Atlantic coast are confined to tidal freshwater and polyhaline regions of the estuary (Table 13.1). In addition, published studies are almost exclusively of low intertidal marshes that are frequently inundated; we know of only one published study of high, infrequently flooded marshes (Table 13.1: Murphy 1991). Other factors that must be considered when interpreting the data presented in Table 13.1 are that these studies employed a variety of sampling methodologies, and that samples were collected in different marsh-surface microhabitats (areas differing sometimes subtly in physical, chemical or biological features). Any of these factors may bias the data. For example, in the studies employing a drop sampler, most samples were taken in a 'marsh edge' habitat, 1–2 m from the water-marsh interface (Zimmerman and Minello 1984). In contrast, Kneib (1991) and Kneib and Wagner (1994) sampled 'interior marsh' 25–90 m from the nearest subtidal habitat using the flume weir. The proximity of a marsh to a subtidal area has an effect on habitat use in that densities of most species decline with distance from the marsh-water interface

(Kneib and Wagner 1994; Peterson and Turner 1994). Therefore, caution is advised in comparing studies in which different microhabitats were sampled.

In a recent review of studies conducted in saltmarshes of the southeast region of the US, Rozas (1993) identified 51 species in 24 families of fishes and seven species in three families of decapod crustaceans that used marsh-surface habitats. The families Cyprinodontidae, Gobiidae, Sciaenidae, Palaemonidae, and Penaeidae contributed the most species to marsh-surface assemblages of saltmarshes in the southeast region (Rozas 1993). Species belonging to these families (except Sciaenidae) also numerically dominated marsh-surface assemblages in the tidal freshwater and brackish marshes that we reviewed (Table 13.1). In addition, members of the family Centrarchidae were important components of assemblages in tidal freshwater environments (Table 13.1). Daggerblade grass shrimp (*Palaemonetes pugio*) and two species of cyprinodonts (gulf killifish, *Fundulus grandis*, on the Gulf coast and mummichog, *Fundulus heteroclitus*, on the Atlantic coast) are among the most abundant macrofaunal species found on the marsh surface, and they were classified as numerically abundant in nearly all of the studies we reviewed (Table 13.2). Other cyprinodonts that were classified as numerically dominant in at least half the studies we reviewed are diamond killifish (*Adinia xenica*) and sheepshead minnow (*Cyprinodon variegatus*) on the Gulf coast, and banded killifish *Fundulus diaphanus* (in tidal freshwater only) on the Atlantic coast. Gobies (naked goby, *Gobiosoma bosc*, and darter goby, *Gobionellus boleosoma*) numerically dominated marsh-surface assemblages only on the Gulf coast (Table 13.2). Blue crab (*Callinectes sapidus*) and penaeid shrimp (mostly brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*) were abundant in most of the habitats sampled (Table 13.2). In the only published work on direct use of Pacific coast marsh, Chamberlain and Barnhart (1994) found threespine stickleback (*Gasterosteus aculeatus*) and gobies (arrow goby, *Clevelandia ios*, and tidewater goby, *Eucyclogobius newberryi*) to be most abundant. However, the elevation of their natural study marsh was relatively high, a factor that may have contributed to the low densities and few species they reported.

### 13.1.4 Patterns of resident versus transient use among marsh microhabitats

Estuarine nekton can be classified into various groups based on ecological affinity (McHugh 1967; Deegan and Thompson 1985). Accordingly, the species listed in Table 13.1 were classified into the three affinity groups (freshwater, estuarine, and estuarine-marine) after Deegan and Thompson (1985) as shown in Table 13.2. Freshwater species generally spawn in freshwater or low salinity regions of the estuary, and because they cannot tolerate high salinities, are usually restricted to the upper estuary. Estuarine species spawn and spend most of their lives within the estuary; they are commonly found throughout the estuary because they can tolerate a wide range of salinity. Estuarine-marine species occur in the estuary primarily as



**Table 13.1** List of numerically dominant fishes and crustaceans (in descending order of abundance) collected on the marsh surface compiled from studies of northern Gulf Mexico and Atlantic coast estuaries. The sampling frequency and duration, gear type, number of sampling sites and the total number of samples taken, salinity regime, dominant marsh vegetation, and the source of information are given for each data set

	Lavaca Bay, TX	Lavaca Bay, TX	Trinity Bay, TX
Fishes:	Naked goby Darter goby Silver perch Pinfish Gulf killifish	Naked goby Bay anchovy Gulf killifish Diamond killifish Pinfish	Sheepshead minnow Gulf killifish Striped mullet Rainwater killifish Bayou killifish
Crustaceans:	Daggerblade grass shrimp Brown shrimp Marsh grass shrimp Blue crab White shrimp	Daggerblade grass shrimp Brown shrimp Blue crab White shrimp Pink shrimp	Daggerblade grass shrimp Blue crab Pink shrimp Brown shrimp
Sampling Frequency & Duration:	2/year (fall and spring) for 1 year	2/year (fall and spring) for 1 year	3/year (spring, summer, and fall) for 1 year
Gear Type:	2.6 m squared drop sampler	2.6 m squared drop sampler	2.6 m squared drop sampler
Sampling Sites (Total Number):	24 (24)	24 (24)	24 (24)
Salinity Regime:	Mesohaline	Mesohaline	Oligohaline
Dominant Vegetation:	<i>Spartina alterniflora</i>	<i>Juncus roemerianus</i>	<i>Scirpus</i> spp
Source:	Zimmerman et al. (1990a)	Zimmerman et al. (1990a)	Zimmerman et al. (1990b)
	Galveston Bay, TX	Christmas Bay/West Bay, TX	Terrebonne Bay, LA
Fishes:	Naked goby Speckled worm eel Pinfish Gulf killifish Blackcheek tonguefish	Darter goby Sheepshead minnow Pinfish Inland silverside Naked goby	Striped mullet Sheepshead minnow Gulf killifish Diamond killifish Inland silverside
Crustaceans:	Daggerblade grass shrimp Blue crab Marsh grass shrimp Brown shrimp White shrimp	Daggerblade grass shrimp Brown shrimp Blue crab White shrimp Pink shrimp	Daggerblade grass shrimp Blue crab White shrimp Brown shrimp
Sampling Frequency & Duration:	3/year (spring, summer, and fall) for 1 year	3/year (spring, summer, and fall) for 1 year	1–3/month for 8 months (April–November)
Gear Type:	2.6 m squared drop sampler	2.6 m squared drop sampler	6 m squared bottomless lift net
Sampling Sites (Total Number):	24 (24)	24 (24)	6 (90)
Salinity Regime:	Mesohaline	Polyhaline	Mesohaline
Dominant Vegetation:	<i>Spartina alterniflora</i>	<i>Spartina alterniflora</i>	<i>Spartina alterniflora</i>
Source:	Zimmerman et al. (1990b)	Zimmerman (1990b)	Rozas and Reed (1993)

**Table 13.1 (continued)**

	Terrebonne Bay, LA	Terrebonne Bay, LA	Terrebonne Bay, LA
Fishes:	Gulf killifish Sheepshead minnow Diamond killifish Striped mullet Bayou killifish	Naked goby Gulf killifish Diamond killifish Bayou killifish Darter goby	Gulf killifish Diamond killifish Sheepshead minnow Naked goby Inland silverside
Crustaceans:	Daggerblade grass shrimp Blue crab Brown shrimp	*Grass shrimp Blue crab	Daggerblade grass shrimp Blue crab Brown shrimp
Sampling Frequency & Duration:	1–3/month for 8 months (April–November)	1/month for 11 months (January–November)	2/month for 1 year
Gear Type:	6 m squared bottomless lift net	Flume	Flume
Sampling Sites (Total Number):	3 (45)	15 (165)	6 (120)
Salinity Regime:	Mesohaline	Mesohaline	Mesohaline
Dominant Vegetation:	<i>Distichlis spicata</i>	<i>Spartina alterniflora</i>	<i>Spartina alterniflora</i>
Source:	Rozas and Reed (1993)	Peterson and Turner (1994)	Rozas (1992)
	Barataria Bay/Caminada Bay, LA	Duplin River, GA	Newport River, NC
Fishes:	Naked goby Darter goby Inland silverside Bay anchovy Gulf menhaden	Mummichog Spotfin killifish **Mullet Spot Sailfin molly	Mummichog Spot Striped killifish Sheepshead minnow Spotfin mojarra
Crustaceans:	Daggerblade grass shrimp Blue crab Brown shrimp White shrimp	Daggerblade grass shrimp White shrimp	***Grass shrimp ***Penaeid shrimp (3 spp) Blue crab
Sampling Frequency & Duration:	1–2/month for 3.5 year (fewer samples in winter)	1–10 (mean = 6)/mo for 2 year (fewer in winter)	1/month for 1 year
Gear Type:	0.5 and 1.2 m squared drop samplers	100 m squared flume weir	Block net
Sampling Sites (Total Number):	Fishes = 309 (309)/crustaceans = 97 (97)	2 (271)	8 (96)
Salinity Regime:	Mesohaline	Polyhaline	Polyhaline
Dominant Vegetation:	<i>Spartina alterniflora</i>	<i>Spartina alterniflora</i>	<i>Spartina alterniflora</i>
Source:	D. M. Baltz, personal communication	Kneib (1991)	Hettler (1989)

Table 13.1 (continued)

	Chickahominy River, VA	Morris Creek, VA	Webbet River/Little River, ME
Fishes:	Mummichog Banded killifish Inland silverside Spottail shiner Pumpkinseed Daggerblade grass shrimp Blue crab	Banded killifish Mummichog Bluegill Pumpkinseed Mosquitofish Daggerblade grass shrimp Blue crab	****Mummichog
Crustaceans:			
Sampling Frequency & Duration:	4/month for 4 month (July–October)	2–4/month for 6–7 months (spring–fall) over 2 year	36–44/5 month (May–September) for 1 year
Gear Type:	Flume net	Flume net	Flume net
Sampling Sites (Total Number):	9 (144)	6 (204)	6 (232)
Salinity Regime:	Tidal freshwater	Tidal freshwater	Polyhaline
Dominant Vegetation:	<i>Peltandra virginica</i>	<i>Peltandra virginica</i>	<i>Spartina patens</i>
Source:	Rozas and Odum (1987)	McIvor and Odum (1988)	Murphy (1991)

\* Peterson and Turner (1994) did not identify grass shrimp (*Palaemonetes* spp.) to species

\*\* Knieb (1991) did not identify mullets (*Mugil* spp.) to species

\*\*\* Hettler (1989) did not enumerate grass shrimp and identified penaeids to genus only

\*\*\*\* Murphy (1991) collected few fish other than mummichogs (six ninespine stickleback, two Atlantic silverside, and one fourspine stickleback), and grass shrimp were only infrequently taken (S. C. Murphy, personal communication)

**Table 13.2** List of numerically dominant fishes and crustaceans collected on the marsh surface of Gulf of Mexico and Atlantic coastal marshes. The frequency with which each species was reported as abundant (FOA) from studies listed in Table 13.1 and its ecological affinity (after Deegan and Thompson 1985) are given

Common name	Scientific name	FOA (%)	Ecological Affinity
<b>Gulf of Mexico</b>			
<i>Fishes</i>			
Gulf killifish	<i>Fundulus grandis</i> Baird & Girard	80	Estuarine
Naked goby	<i>Gobiosoma bosc</i> (Lacepede)	60	Estuarine
Sheepshead minnow	<i>Cyprinodon variegatus</i> Lacepede	50	Estuarine
Diamond killifish	<i>Adinia xenica</i> (Jordan & Gilbert)	50	Estuarine
Inland silverside	<i>Medinia beryllina</i> (Cope)	40	Estuarine
Pinfish	<i>Lagodon rhomboides</i> (Linnaeus)	40	Estuarine
Darter goby	<i>Gobionellus boleosoma</i> (Jordan & Gilbert)	40	Estuarine
Striped mullet	<i>Mugil cephalus</i> Linnaeus	30	*Estuarine–Marine
Bayou killifish	<i>Fundulus pulvereus</i> (Evermann)	30	Estuarine
Bay anchovy	<i>Anchoa mitchilli</i> (Valenciennes)	20	Estuarine–Marine
Blackcheek tonguefish	<i>Symphurus plagiusa</i> (Linnaeus)	10	*Estuarine–Marine
Speckled worm eel	<i>Myrophis punctatus</i> Lutken	10	Estuarine–Marine
Rainwater killifish	<i>Lucania parva</i> (Baird & Girard)	10	Estuarine
Silver perch	<i>Bairdiella chrysoura</i> (Lacepede)	10	Estuarine–Marine
Gulf menhaden	<i>Brevoortia patronus</i> Goode	10	Estuarine–Marine
<b>Crustaceans</b>			
Daggerblade grass shrimp	<i>Palaemonetes pugio</i> Holthius	100	Estuarine
Blue crab	<i>Callinectes spidus</i> Rathbun	100	Estuarine–Marine
Brown shrimp	<i>Penaeus aztecus</i> Ives	90	Estuarine–Marine
White shrimp	<i>Penaeus setiferus</i> (Linnaeus)	60	Estuarine–Marine
Pink shrimp	<i>Penaeus duorarum</i> Burkenroad	30	Estuarine–Marine
Marsh grass shrimp	<i>Palaemonetes vulgaris</i> (Say)	20	Estuarine
<b>Atlantic coast</b>			
<i>Fishes</i>			
Mummichog	<i>Fundulus heteroclitus</i> (Linnaeus)	100	Estuarine
Spot	<i>Leiostomus xanthurus</i> Lacepede	40	Estuarine–Marine
Pumpkinseed	<i>Lepomis gibbosus</i> (Linnaeus)	40	Freshwater
Banded killifish	<i>Fundulus diaphanus</i> (Lesueur)	40	Freshwater
Spotfin killifish	<i>Fundulus luciae</i> (Baird)	20	Estuarine
Inland silverside	<i>Menidia beryllina</i> (Cope)	20	Estuarine
Sheepshead minnow	<i>Cyprinodon variegatus</i> Lacepede	20	Estuarine
Striped killifish	<i>Fundulus majalis</i> (Walbaum)	20	Estuarine
Sailfin molly	<i>Poecilia latipinna</i> (Lesueur)	20	Freshwater
Bluegill	<i>Lepomis macrochirus</i> Rafinesque	20	Freshwater
Spotfin mojarra	<i>Eucinostomus argenteus</i> Baird & Girard	20	Estuarine–Marine
Spottail shiner	<i>Notropis hudsonius</i> (Clinton)	20	Freshwater
Mosquitofish	<i>Gambusia holbrooki</i> (Girard)	20	Freshwater
<b>Crustaceans</b>			
Daggerblade grass shrimp	<i>Palaemonetes pugio</i> Holthius	80	Estuarine
Blue crab	<i>Callinectes sapidus</i> Rathbun	60	Estuarine–Marine
White shrimp	<i>Penaeus setiferus</i> (Linnaeus)	20	Estuarine–Marine

\* In marsh–surface habitats, these fishes fit the definition of Estuarine–Marine species, but were previously classified as Marine species by Deegan and Thompson (1985)

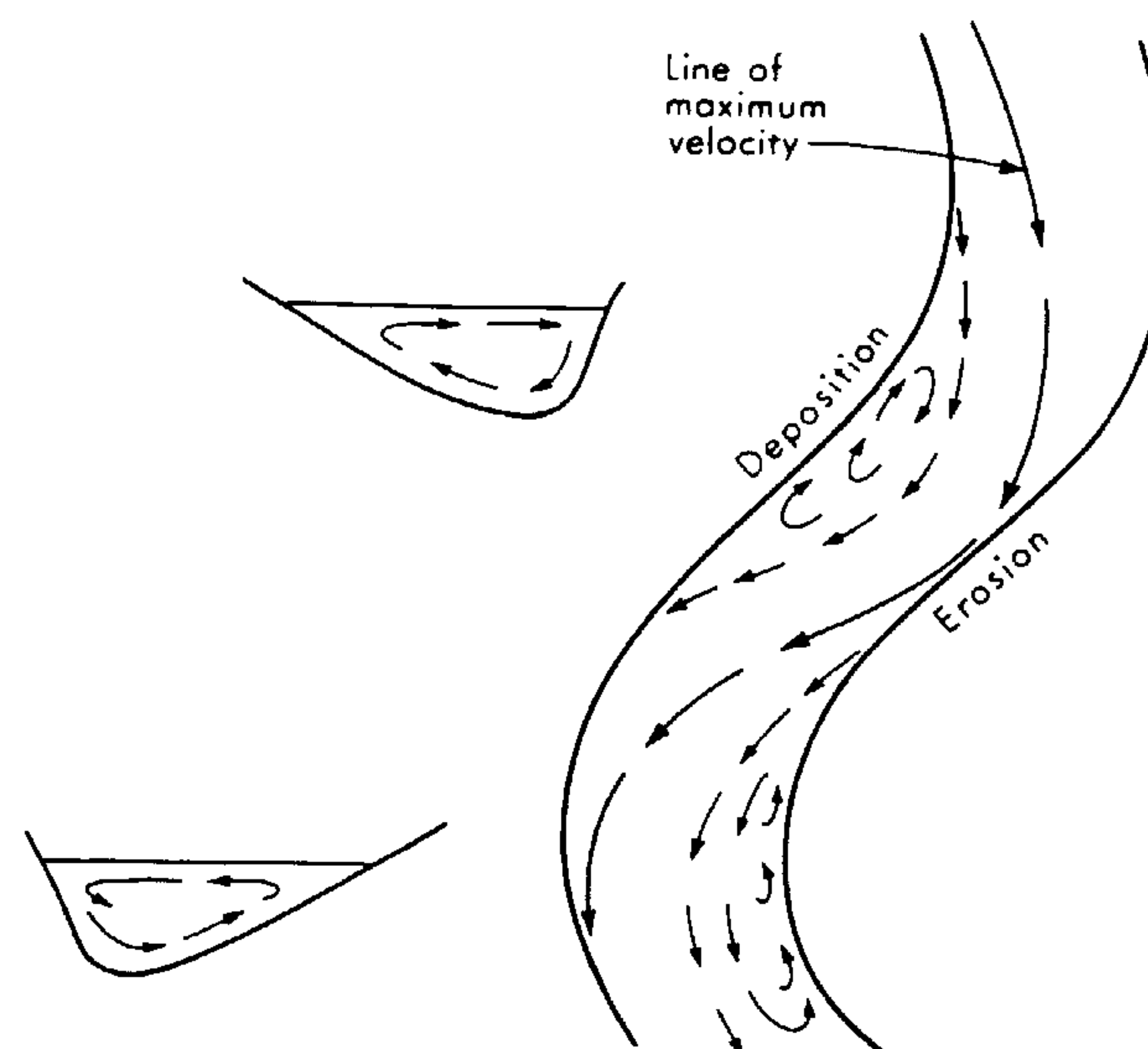
young of the year; they usually spawn in nearshore or marine areas. Many of the species that belong to the estuarine-marine group support important coastal fisheries.

Marsh-surface assemblages of fishes on both coasts were dominated by estuarine species, except in tidal freshwater environments of the Atlantic coast, where freshwater species predominated (Table 13.2). Most species in these two affinity groups (estuarine and freshwater) are year-round residents of tidal marshes. Another estuarine species, the daggerblade grass shrimp, was the most abundant crustacean using the marsh surface. However, most other numerically dominant crustaceans associated with marsh-surface habitats (e.g. blue crab and penaeid shrimp) belong to the estuarine-marine group.

### 13.2 SMALLER SCALE CORRELATES OF PATTERNS OF COMPOSITION AND NUMERICAL ABUNDANCE

#### 13.2.1 Subtidal geomorphology

Because nekton using the marsh surface must leave this habitat with the ebb tide, features of the subtidal environment are also relevant to understanding fish assemblages using marsh-surface habitat. Stream meanders and associated depositional and erosional banks are a universal feature of streams (Morisawa 1968; Garofalo 1980). Depositional and erosional banks resulting from stream sinuosity differ most obviously in depth (Figure 13.2), but also in slope, current velocity (Morisawa 1968), substrate particle size (Hynes 1970), concentration of detrital size fractions (Pickral and Odum 1977), and presence or absence of submerged aquatic vegetation (personal observation of the authors). Working in the tidal freshwater portion of the Chickahominy River, Virginia (tidal range 0.7 m, McIvor and Odum (1988) used flume nets to sample nekton at marsh-surface sites adjacent to shallow depositional and steeper erosional banks. They found that marsh-surface sites adjacent to depositional banks supported significantly higher numbers of nekton. Both lower encounter rates with piscivorous predators (assessed from tethering experiments) and higher food availability (assessed from feeding experiments) in the depositional subtidal zone are likely mechanisms producing this pattern. Analogous studies have not been conducted in more saline portions of estuaries, or in other regions where tidal ranges are smaller. McIvor and Odum (1988) postulated that because meanders and associated depositional and erosional banks are a universal geomorphological feature of streams (Morisawa 1968; Garofalo 1980), the results of their study were likely to apply to tidal creeks and associated estuarine marshes in general. However, the results may not hold in Gulf coast marshes where tidal ranges seldom exceed 0.30 m, where the differences between depositional and erosional banks are less pronounced, and where the marsh-water interfaces are more likely due to pond formation from subsidence



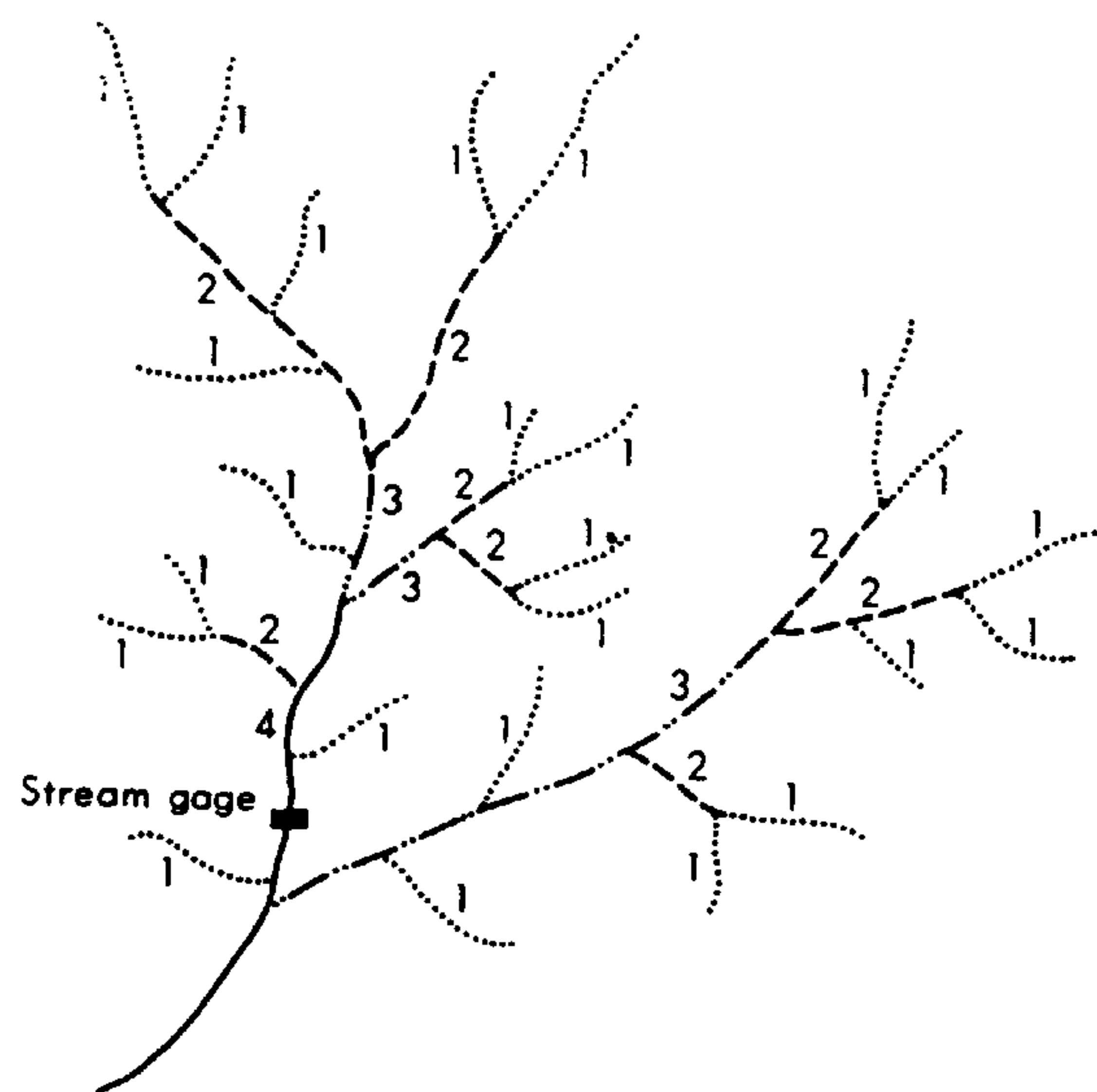
**Figure 13.2** Meandering stream reach, showing depositional and erosional banks. Transverse sketches show lateral movement of water in the bends. (Reproduced by permission from Morisawa 1968)

(Sasser et al. 1986; Reed 1991) than from classic channel development. More research is needed to ascertain the generality of the relative importance of bank profile in influencing intertidal marsh use by nekton.

#### 13.2.2 Stream order

Weinstein (1979), in an analysis of nursery areas for nekton, first proposed that 'marshes fill up backwards during recruitment'. This statement might be interpreted to imply that smaller order streams (*sensu* Horton 1945, Figure 3) have higher abundances of nekton. Rozas and Odum (1987a) tested this hypothesis in tidal freshwater marshes of the Chickahominy River, Virginia. Using flume nets, they sampled nekton on intertidal marshes adjacent to stream orders 2 (headwater), 3 (main creek), and 4 (river). Though crustacean numbers did not differ significantly between marshes, fish numbers were significantly greater on headwater and main creek marshes than on river marshes. These investigators hypothesized that the relationship between marsh stream order and fish abundance may be due in part to the distribution of submerged aquatic vegetation (SAV) in tidal marsh creeks. SAV





**Figure 13.3** Hierarchy of stream ordering after Horton 1945. Numbers and pattern indicate order of respective segments. The watershed is fourth-order. (Reproduced by permission from Morisawa 1968)

decreased in abundance (as did fish abundance) with increasing stream order in these particular streams. The presence of SAV in tidal creeks may enhance the refuge value and food resources of those creeks, and thus, the habitat value of adjacent tidal marshes (Rozas and Odum 1987a).

Even smaller (and of lower stream order) than headwater creeks are intertidal rivulets, small creeks or channels that drain the marsh surface. Though tens of centimeters lower than the general marsh surface, rivulets begin to flood earlier on the rising tide and remain inundated longer than the remainder of the marsh surface on the ebb tide. Flumes placed along rivulets in a tidal freshwater marsh contained three times the number and 14 times the biomass of fishes as flumes placed on depositional creekbanks (Rozas et al. 1988). Rivulets may serve as preferred corridors between marsh surface and tidal channel habitats for natant organisms because of the benefits associated with a longer period of inundation, i.e. more extended access to food in periodically flooded habitats, and protection from predators requiring deeper waters for effective foraging.

One other investigator has documented patterns of nekton use of marsh surfaces that support the stream order hypothesis, and extend it from tidal freshwater to

saline marshes. Hettler (1989) used block nets (essentially flume nets without side or back partitions) to compare nekton use of two polyhaline marsh sites in the Newport River estuary, North Carolina. Channel sites of order 3 were bordered by steeply sloping subtidal areas, whereas rivulet sites (order 1) were bordered by shallow depositional subtidal profiles. Significantly more individuals were found in rivulet sites, although more species were found in channel sites. During summer, the number of individuals from the rivulet habitat was an order of magnitude greater than the number collected from the channel marsh, due to the abundance of resident killifishes (Hettler 1989).

### 13.2.3 Submergence time (elevation)

Flooding duration or marsh submergence time obviously influences its use by nekton, because aquatic organisms can occupy the habitat only when it is flooded. (Exceptions include larval or postlarval forms that can survive in small water-filled depressions or crab burrows.) Submergence time is affected by several factors including marsh-surface elevation, tidal regime, and meteorological events. However, within the same marsh system, surface elevation has the most influence on flooding duration and habitat availability. Therefore, elevation may be an important factor controlling the distribution of animals among marsh-surface microhabitats (Minello et al. 1991; Rozas and Reed 1993). Rozas and Reed (1993) examined the influence of submergence time on habitat selection by nekton by comparing densities of natant organisms in three habitats having different elevations (high *Distichlis* marsh, medium *Spartina alterniflora* marsh, and low *S. alterniflora* marsh). Penaeid shrimp (white shrimp and brown shrimp) were most abundant in the low *Spartina* marsh, which flooded longer and deeper than the other habitats that were sampled. Minello and colleagues (1994) reported densities of daggerblade grass shrimp and brown shrimp 1.2–4.3 times higher on low than high *S. alterniflora* marsh, but found no effect of elevation on the abundance of white shrimp. Similarly, Kneib and Wagner (1994), working in a *Spartina alterniflora* marsh in Georgia, found apparent habitat preference for most species for sites of lower elevation that were closer to permanent tidal channels. An exception was the spotfin killifish *Fundulus luciae*, a high marsh specialist.

Extended periods of marsh submergence should benefit organisms that use the marsh surface, especially when food and cover are less abundant in subtidal habitats (Weisberg and Lotrich 1982; Minello and Zimmerman 1991). Kneib (1993) found that for larval mummichogs, growth was positively related and mortality rates negatively related to flooding duration in a Georgia saltmarsh. He attributed the higher growth rates and greater survival during longer flooding periods to increased prey availability, primarily benthic harpacticoid copepods. Mummichogs had largely unrestricted access to prey when the marsh surface was flooded, which was 16–32% of a given 24 h period at this location, depending on marsh elevation and tidal conditions.

Surface elevation may also indirectly affect habitat use by influencing prey densities and structural characteristics of the marsh surface. The distribution of benthic infauna in marshes is closely tied to surface elevation (Teal 1958; Cammen 1976; Fell et al. 1982; Kneib 1984; Bishop and Hackney 1987; Kneib 1992). Even subtle differences in marsh-surface topography may affect the abundance of infaunal prey and their availability to fish and crustacean predators that exploit the habitat. In addition, plant stem density is generally inversely related to flooding duration. Therefore, stem density in low marsh is relatively sparse (Mendelssohn and McKee 1988), a factor that may enhance the foraging opportunity for small natant predators (West and Williams 1986; Rozas and Reed 1993). Sparse vegetation may provide more foraging surface than unvegetated areas, yet may interfere less with the movement and foraging activity of predators than thick vegetation (Vince et al. 1976; Van Dolah 1978; West and Williams 1986).

Although high marsh floods infrequently and for shorter periods of time, it is exploited by some natant species. During a rising tide, killifishes follow the advancing edge of flooding water across the marsh surface and are concentrated in high marsh at high tide (Kneib 1976, 1984; Rozas and Reed 1993). If the risk of stranding can be overcome, exploiting the high marsh may have several advantages. High marsh environments may contain more food than low marsh because prey are exposed to fewer predators and for shorter periods of time (Kneib 1984; 1993). High marsh also has denser vegetation and shallower water than low marsh, factors that may offer greater protection from piscivorous predators. In addition, resident estuarine species that spawn on the marsh surface may select high marsh for suitable spawning sites (Greeley and MacGregor 1983).

High marsh pools differ from surrounding vegetated high marsh in providing permanently flooded microhabitat for resident fishes and crustaceans. Such pools are common features in New England marshes (Redfield 1972), where they act as habitat, primarily for resident fishes (several species of killifish, silversides, a goby, freshwater eels (*Anguilla rostrata*)) (Able et al. 1995, Chapter 14). Additionally, such pools serve as overwintering habitat for mummichogs (Smith and Able 1994). Mummichogs and blue crabs occupied an analogous pool in a North Carolina salt marsh (Kneib 1982).

#### 13.2.4 Edge (drainage density)

The proximity of a marsh to subtidal habitat is important because most aquatic organisms using the marsh surface are confined to subtidal areas at low tide, and there seems to be a limit to the distance some organisms will travel into the marsh from open-water (Peterson and Turner 1994). Edge habitat, i.e. the interface between marsh and open-water, often originates and is configured in fundamentally different ways in Atlantic coast marshes (and other environments with moderate tidal ranges), and in Gulf coast marshes. In the former, edge is related primarily to drainage density or the complexity of the channel network of the system, itself a

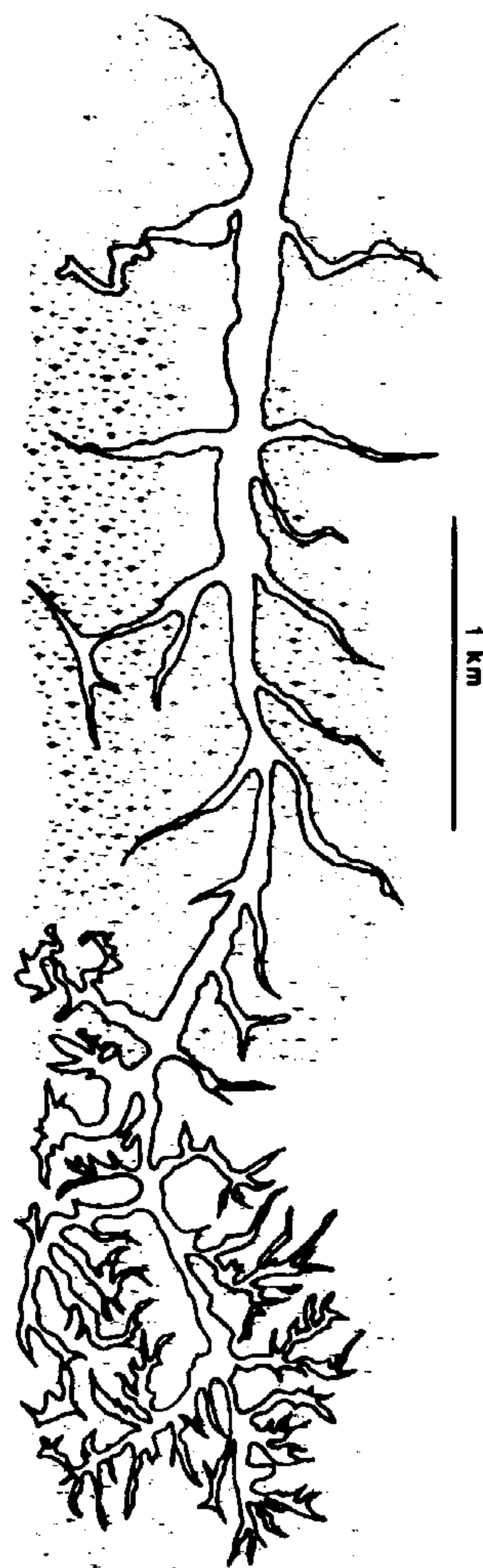
function of marsh age. Findings from saltmarshes around Sapelo Island, Georgia suggest that drainage density decreases as marshes become older (Frey and Basan 1978). Additionally, high drainage density habitats tend to be associated with headwaters, whereas areas of low drainage density usually occur near the mouths of tidal channels (Figure 13.4) (Kneib 1994). On the Gulf coast, especially in areas undergoing coastal submergence, much of the edge habitat, which occurs in the marsh interior away from channels, is created by pond formation (Sasser et al. 1986; Reed 1991).

Nekton are not evenly distributed over the marsh surface at high tide. Most species are concentrated in the emergent vegetation near the marsh-water interface (edge habitat) (Baltz et al. 1993; Peterson and Turner 1994). Species using interior marsh remote from subtidal habitats are mostly estuarine species belonging to two families, Cyprinodontidae and Palaemonidae (Peterson and Turner 1994). These two families include some of the most abundant species exploiting the marsh surface (e.g. daggerblade grass shrimp, gulf killifish, mummichog, and sheepshead minnow). Few species in the estuarine-marine affinity group seem to venture very far from the marsh edge. Striped mullet and blue crab may be the only species in this group that use interior marsh on the Gulf coast (Rozas and Reed 1993; Peterson and Turner 1994), whereas mullet, spot, white shrimp, and blue crab exploit such habitat on the Atlantic coast (Kneib 1991). Even so, many of the species that have been collected from interior marsh may be found in greater densities in edge habitats. Distance traveled and the timing of movement across the marsh surface by nekton may be dependent on organism size and swimming ability (Kneib and Wagner 1994). Relatively large animals and strong swimmers incur less risk of stranding by exploiting the marsh surface than small organisms and weak swimmers, and therefore may venture farther away from the edge into interior marsh. Relatively large, strong swimmers would also be expected to reach interior marsh habitats sooner during the tidal cycle (Kneib and Wagner 1994).

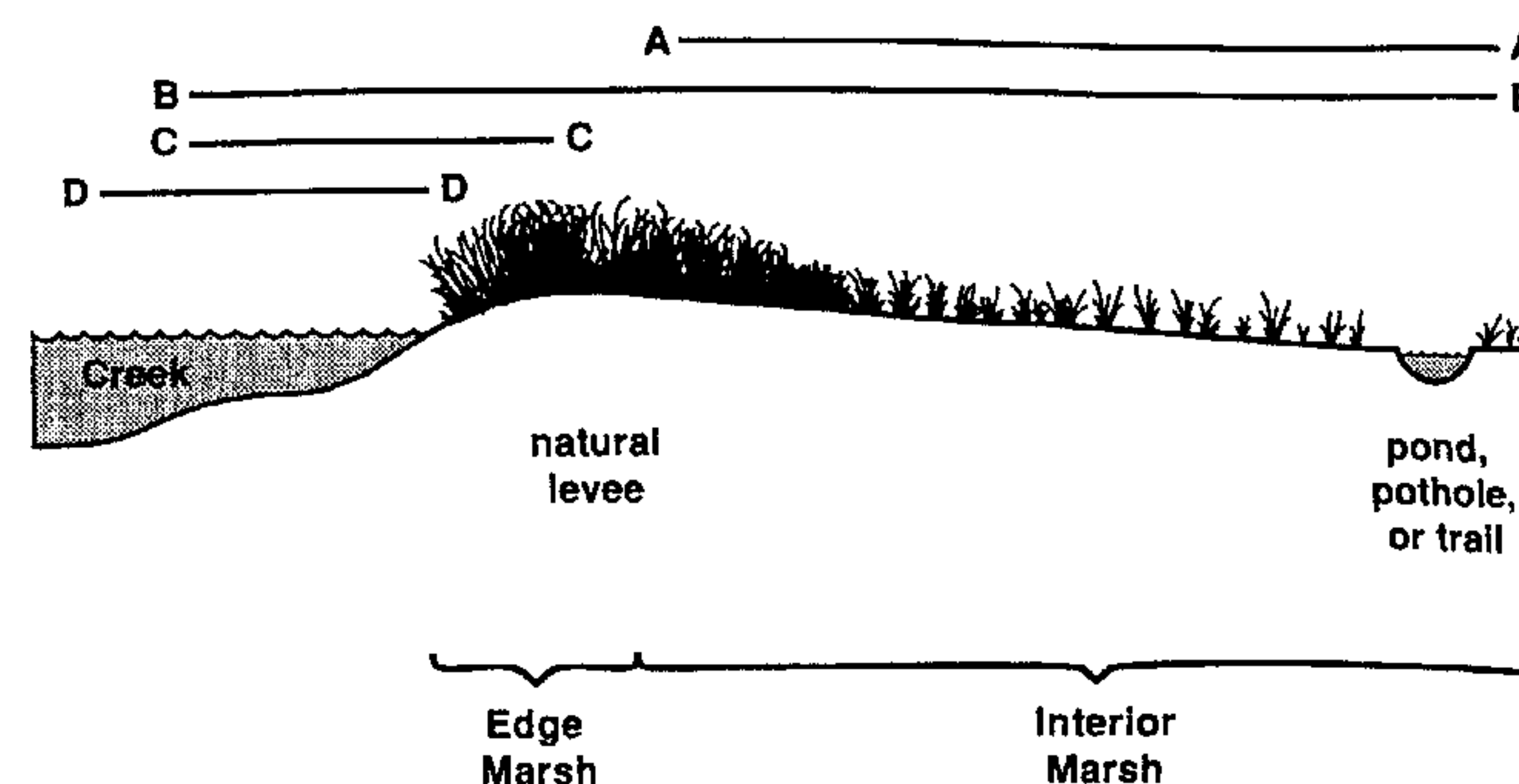
Peterson and Turner (1994) identified four patterns of marsh surface use based on the frequency of occurrence of nekton in portions of a Louisiana marsh differing in elevation, distance from open water, vegetation density, and proximity to marsh pools or potholes (Figure 13.5). Their data strongly suggest that nekton species differ substantially in their use of different portions of the marsh surface. This question of use of interior, often higher elevation habitat versus edge, generally low elevation habitat has not been fully addressed.

Because most species (and almost all fishery species) exploit marsh edge habitat, secondary productivity may be related to the amount of edge habitat contained in a marsh system (Zimmerman and Minello 1984; Zimmerman et al. 1991; Peterson and Turner 1994). Kneib (1994) used flume weirs to compare fish densities at a high and a low drainage density site along the Duplin River, Georgia. Over 19 months, he consistently found higher fish densities at the site with high drainage density. Minello and colleagues (1994) experimentally addressed the question of the importance of edge in determining standing stocks of nekton in a





**Figure 13.4** Geomorphology of drainage channels in a saltmarsh on Sapelo Island, GA. Note the higher density of drainages in the headwater portion. (Reproduced by permission from Kneib 1994)



**Figure 13.5** Patterns of nekton use of marsh habitats in a Louisiana marsh. A = interior marsh residents, species that use the marsh interior and retreat to potholes, muskrat trails, or small ponds at low tide; B = interior marsh users, species that use interior marshes but retreat to the creek edge at low tide; C = marsh edge users, species that use only marsh edge habitat; D = marsh subtidal group, open-water species not utilizing the marsh surface. (Reproduced by permission from Peterson and Turner 1994)

Texas marsh. They compared nekton densities at sites within a transplanted *Spartina alterniflora* marsh where channels were added, versus control sites without added channels. Adding channels (and increasing edge habitat) in the *Spartina* marsh dramatically increased densities of brown shrimp and white shrimp near the channels by a factor of 4.6 to 13 (Minello et al. 1994). Adding channels also significantly raised the densities of polychaete worms and daggerblade grass shrimp in the marsh edge. These animals are preyed on by small fishes, blue crabs, and brown shrimp (Harrington and Harrington 1961; Gleason and Wellington 1988; Minello et al. 1989; Thomas 1989; McTigue and Zimmerman 1991).

At a regional scale, densities of penaeid shrimp were much higher in marsh surface vegetation in Galveston Bay in the Gulf of Mexico (Zimmerman and Minello 1984) than in saltmarsh habitats in South Carolina (Wenner and Beatty 1993). Such differences are consistent with an explanation of greater edge in the reticulated marshes in Galveston Bay (Zimmerman and Minello 1984). However, other differences, including greater duration of marsh flooding (seasonal in Galveston Bay), are likely also involved (Wenner and Beatty 1993; Rozas 1995).

### 13.3 LANDSCAPE-LEVEL PROCESSES

#### 13.3.1 Linkage of adjacent habitats

Ecologists and managers are increasingly interested in linkages between adjacent ecosystems or habitats. Linkages between intertidal marshes and adjacent subtidal

habitats can be viewed in two fundamentally different ways: (1) the systems are coupled by the exchange of energy and nutrients, and (2) the systems are linked because many organisms make direct use of both as habitat.

The focus on habitat linkages derives from the predictable use by some nekton of two or more adjacent habitats, and the inference that both habitats contribute to the growth and survival of these organisms. This view is based on studies of nekton abundance in adjacent habitats under different tidal regimes. Some organisms common in permanent subtidal habitats at ebb tide are found primarily within intertidal habitats on flood tides. Such distributions are indicative of active movement between adjacent habitats as the intertidal habitats are alternately flooded and drained by tidal fluctuation. A wide variety of fishes and crustaceans exhibit this pattern of habitat use (see 13.1.2). Of these species, the mummichog and brown shrimp have been experimentally shown to benefit from use of intertidal habitat. For instance, mummichogs caged in permanent subtidal waters grew more slowly than others allowed access to the intermittently flooded marsh surface (Weisberg and Lotrich 1982). In a similar experiment, brown shrimp held in cages containing *S. alterniflora* had significantly higher growth rates than those in cages devoid of vegetation (Minello and Zimmerman 1991).

It can be concluded that despite only being available to nekton for a few hours once or twice a day (or sometimes seasonally), the vegetated intertidal marsh surface has high habitat 'value' for a wide variety of species of nekton. Whereas some of the killifishes spawn here (Taylor et al. 1979; Able 1984), most organisms probably gain food or shelter, or both, from this highly structured, relatively shallow environment. Gulf killifish (Rozas and LaSalle 1990), mummichogs (Butner and Brattstrom 1960; Rozas et al. 1988), freshwater killifish (Rozas et al. 1988), and spot (Miller and Dunn 1980) contain more food when leaving than when entering the marsh surface. Gulf killifish feed on a wide range of benthic invertebrates and detritus while on the marsh surface (Harrington and Harrington 1961; Rozas and LaSalle 1990). Blue crabs in a Georgia marsh feed intertidally on fish and non-portunid crabs (Fitz and Wiegert 1991). Additional indirect evidence of the probable use of flooded intertidal habitats is provided by a comparison of the state of the tidal cycle in which marsh nekton contain the most food in their gut. Both juvenile silver perch (*Bairdiella chrysura*) and blue crabs contain fuller stomachs during or immediately following peak tidal inundation than individuals of those species taken at other times in the tidal cycle (Kleypas and Dean 1983; Ryer 1987).

Quantitative data on the refuge value of intertidal saltmarshes compared with that of adjacent habitats are largely lacking. However, Minello (1993) determined experimentally that tethered brown shrimp exhibited higher survival rates in saltmarsh (and seagrass habitats) than on unvegetated sand bottom in a Texas bay. Most of our hypotheses about the refuge value of saltmarsh habitat are presently extrapolated from assessments of refuge value derived from other habitat comparisons, e.g. submersed aquatic vegetation versus bare substrate (Zimmerman

and Minello 1984; Rozas and Odum 1987b), or from laboratory experiments (e.g. Minello and Zimmerman 1983).

### 13.3.2 Nekton as agents of export from the intertidal marsh

Coupling of adjacent habitats by the exchange of materials may be controlled strictly by physical processes, may be mediated by the movement of biological organisms, or a combination of both. Physical linkages are far better documented. The best understood examples include the one-way downslope movement of dissolved and particulate matter mediated by physical factors including runoff and groundwater flow (e.g. Fisher and Likens 1973; Valiela et al. 1992). Bidirectional movement of inert materials, nutrients and carbon, on and off the marsh surface by the tides and exchange with estuarine waters are also reasonably well known, though spatially and temporally complex (e.g. Odum et al. 1979; Nixon 1980).

Mobile organisms can also be nutrient and carbon vectors. However, the best estimates of movement of nutrients and organic matter by fishes come from other ecosystems. Bray and colleagues (1981) showed that planktivorous damselfish (*Chromis punctipinnis*) imported  $8 \text{ g C m}^{-2} \text{ a}^{-1}$  from the pelagic zone to a California rocky reef community. Meyer and Schultz (1985) demonstrated that French and white grunts (*Haemulon flavolineatum*, *H. plumieri*) imported an average of  $76 \text{ g POC (particulate organic carbon) m}^{-2} \text{ a}^{-1}$  from seagrass beds to a coral reef community. Analogous quantitative data on nekton as vectors of nutrient movement between subtidal and intertidal marsh habitats are lacking, though often hypothesized or inferred (McIvor and Odum 1988; Rozas and LaSalle 1990; Fitz and Wiegert 1991; Kneib and Wagner 1994). At the estuarine scale, Deegan (1993) has estimated that gulf menhaden (*Brevoortia patronus*) export  $22.5 \text{ g C m}^{-2} \text{ a}^{-1}$  from Fourleague Bay, LA to the Gulf of Mexico. This is roughly 5–10% of the primary production of this estuarine area.

## 13.4 SUMMARY

Geomorphological and hydrological features of saltmarshes (subtidal profile, stream order, flooding duration, elevation, drainage density and amount of edge) directly affect both the degree and patterns of use of marsh surface habitat by nekton. Whereas we understand the broad general patterns of each of these factors alone in specific locations, we have a poor understanding of how the factors interact to affect marsh surface use and microhabitat selection. Most importantly, we know little of how the patterns and interactions (and rankings) of factors differ regionally. Further, our understanding of the linkages between intertidal and subtidal habitats is in its infancy. Future research should address how these linkages affect the population dynamics (recruitment success, growth, mortality) of the most abundant resident and transient species. More studies of direct marsh use are



needed, especially on the Pacific and Atlantic coasts, and future investigations should include regional comparisons of similar microhabitats using identical quantitative sampling methods. Research is also needed on the relative importance of nekton as vectors of carbon and nutrient exchange between adjacent intertidal and subtidal habitats.

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